Differential temporal beta-diversity patterns of native and non-native arthropod species in a fragmented native forest landscape

Matthews, Thomas; Sadler, Jonathan; Carvalho, Rui; Nunes, Rui; Borges, Paul A V

DOI:
10.1111/ecog.03812

Document Version
Peer reviewed version

Citation for published version (Harvard):
Matthews, T, Sadler, J, Carvalho, R, Nunes, R & Borges, PAV 2019, 'Differential temporal beta-diversity patterns of native and non-native arthropod species in a fragmented native forest landscape', *Ecography*, vol. 42, no. 1, pp. 45-54. https://doi.org/10.1111/ecog.03812

Journal: Ecography R2

Differential temporal beta-diversity patterns of native and non-native arthropod species in a fragmented native forest landscape

Thomas J. Matthews*[1, 2,3], Jon Sadler[1], Rui Carvalho[2], Rui Nunes[2,4], Paulo A. V. Borges[2,4,5]

[1]GEES (School of Geography, Earth and Environmental Sciences), University of Birmingham, Birmingham, B15 2TT

[2]CE3C – Centre for Ecology, Evolution and Environmental Changes/Azorean Biodiversity Group and Universidade dos Açores – Depto de Ciências Agráriase Engenharia do Ambiente, PT-9700-042, Angra do Heroísmo, Açores, Portugal.

[3]Birmingham Institute of Forest Research, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK

[4]IUCN Mid-Atlantic Island Invertebrates Specialist Group

[5]IUCN SSC Species Monitoring Specialist Group

*Correspondence author. Email: txm676@gmail.com

An important factor that hinders the management of non-native species is a general lack of information regarding the biogeography of non-natives, and, in particular, their rates of turnover. Here, we address this research gap by analysing differences in temporal beta-diversity (using both pairwise and multiple-time dissimilarity metrics) between native and non-native species, using a novel time-series dataset of arthropods sampled in native forest fragments in the Azores. We use a null model approach to determine whether temporal beta-diversity was due to deterministic processes or stochastic colonisation and extinction events, and linear modelling selection to assess the factors driving variation in temporal beta-diversity between plots. In accordance with our predictions, we found that the temporal beta-diversity was much greater for non-native species than for native species, and the null model analyses indicated that the turnover of non-native species was due to stochastic events. No predictor variables were found to explain the turnover of native or non-native species. We attribute the greater turnover of non-native species to source-sink processes and the close proximity of anthropogenic habitats to the fragmented native forest plots sampled in our study. Thus, our findings point to ways in which the study of turnover can be adapted for future applications in habitat island systems. The implications of this for biodiversity conservation and management are significant. The high rate of stochastic turnover of non-native species indicates that attempts to simply reduce the populations of non-native species

in situ within native habitats may not be successful. A more efficient management strategy would be to interrupt source-sink dynamics by improving the harsh boundaries between native and adjacent anthropogenic habitats.

Keywords: Invasive species, beta-diversity, turnover, theory of island biogeography for exotic species, island biogeography, fragmentation, habitat island

Introduction

The introduction, spread and establishment of species outside of their native range can result in substantial changes to natural ecosystems (Mooney and Hobbs 2000, Dyer et al. 2017), sometimes including the local and/or regional extirpation of native species (Clavero and García-Berthou 2005, Bellard et al. 2016). Furthermore, the global rate of transfer and mixing of species between native and non-native ranges does not show any signs of decreasing (Seebens et al. 2017). We use the term 'non-native' throughout this study and we define such species simply as those that are present in an area outside of their native range as a result of human actions (Blackburn et al. 2016), which on islands is generally a consequence of commerce, gardening, agriculture and forestry (Whittaker and Fernández-Palacios 2007).

Indeed, the impact of non-native species, and particularly invasive species (a subset of non-native species), is variable but it does appear to be more acute on islands (Blackburn et al. 2004, Whittaker and Fernández-Palacios 2007, Bellard et al. 2016, but see Sax et al. 2002). A key component of assessing the impact of non-native species in island systems involves the development, and testing, of (island) biogeographical theories and models relevant to them (Pyšek 1998, Blackburn et al. 2008, 2016, Burns 2015). For example, in their fifty 'fundamental questions in island biology', Patiño et al. (2017) recently highlighted that understanding how the impacts of non-native species differ from those of naturally colonising species is a key question in their management.

Burns (2015) has started this process via a recently introduced extension of MacArthur and Wilson's (1967) equilibrium theory of island biogeography (ETIB), which he termed a 'theory of island biogeography for exotic species' (herein, 'TIBE'). TIBE is a graphical island biogeographic model that makes a variety of different predictions regarding the species richness and turnover of native and non-native species (Burns 2015). This was a useful advance as little is known about the turnover patterns of non-natives. However, the analysis of turnover dynamics of non-natives has so far only been studied in the context of true

islands, i.e. islands surrounded by a matrix of water (Whittaker and Fernández-Palacios 2007, Burns 2015). In contrast, the knowledge of turnover patterns for non-native species in habitat islands, i.e. patches of natural habitat surrounded by a matrix of often human dominated habitats (see Matthews 2015), is lacking. Such knowledge is important as the destruction and fragmentation of natural habitat is widely recognised as the leading driver of contemporary species extinctions (e.g. Sala et al. 2000) and also as an important driver of extinction debt (Triantis et al. 2010). Moreover, there has been an increasing recognition of the synergistic effects of the different drivers of species loss (e.g. habitat loss, climate change and invasive species; e.g. Didham et al. 2007, Ferger et al. 2017, Karp et al. 2018). As with true islands, we predict that the turnover of non-native species will be greater than for native species in habitat fragments. However, in true islands the matrix (water) can generally be ignored, whilst in habitat island systems it is possible that the surrounding matrix contributes to turnover patterns within habitat islands. As many non-native species have strong affinities to human-dominated habitats, that is, they are generalists or human habitat specialists (McKinney and Lockwood 1999, Borges et al. 2008, 2010), the presence of non-native species within habitat islands of native habitat is theorised to be driven by stochastic source-sink mass effect dynamics as a result of human disturbance (Williamson 1996, Sgarbi and Melo 2017). Non-native species, which should therefore be less adapted to the conditions within the sink habitat, should have a higher risk of extinction and turnover (MacArthur and Wilson 1967). This possibility has not previously been examined in habitat islands.

A variety of methods have been employed to analyse turnover in the island literature (e.g. Russell et al. 1995, Whittaker et al. 2000, Burns 2015), mostly based on the summation of raw numbers (e.g. number of extinction events). However, another, and arguably more statistically robust, way of analysing temporal changes in species assemblages uses dissimilarity indices, which allow researchers to partition out the effect of richness differences between samples (Baselga 2010, Baselga et al. 2015). One such approach is to use the framework of temporal beta-diversity. Beta-diversity provides a measure of the differences in the composition of communities, and is usually calculated in a spatial context, e.g. to assess how composition changes across a set of sites or along an ecological gradient (Anderson et al. 2011). Temporal beta-diversity is a similar concept, where beta-diversity is calculated for the same location at different times, and in conjunction with a suitable null model the analysis of temporal beta-diversity can be used to determine whether changes in assemblages across time are due to deterministic processes or stochastic colonisation and

extinction events (Baselga et al. 2015). Temporal beta-diversity *sensu stricto* has been much less studied relative to spatial beta-diversity (but see Baselga et al. 2015, Tonkin et al. 2017). Beta-diversity can be calculated using a variety of different approaches (see Anderson et al. 2011) and in this study we focus on the use of dissimilarity indices to calculate beta-diversity, in particular Sørensen dissimilarity. Recent work has partitioned the Sørensen index into turnover and nestedness-resultant dissimilarity / richness difference components (Baselga 2010, 2012, Carvalho et al. 2012).

In this study, we use a unique time-series dataset of arthropods sampled in native forest fragments over five years in the Azores (see Borges et al. 2017) to investigate the differences in turnover dynamics of native and non-native species. Using TIBE and past studies on island theory in habitat islands (e.g. Matthews 2015) as theoretical frameworks, we make two predictions. First, based on the above points, we predict that temporal beta-diversity will be greater for non-native species than for native species (Prediction 1). We use a null model approach to determine whether turnover of species through time was due to deterministic processes or stochastic colonisation and extinction events, and linear modelling selection to assess if any factors (i.e. elevation, climate, disturbance) are driving variation in temporal beta-diversity between plots. Second, as the invasion process is predicted to be on-going (see Burns 2015, Seebens et al. 2017), based on the TIBE we predict that colonisation rate will be greater than extinction rate for non-native species, whilst colonisation rate will be roughly equivalent to extinction rate for native species (Prediction 2).

Our dataset is ideal for examining temporal beta-diversity patterns of native and non-native species in habitat islands as the regular census interval allows us to accurately describe colonisation and extinction events (and thus turnover), and the Azorean arthropod fauna contains a high proportion of non-native species (Borges et al. 2010). Confirming or invalidating these predictions will enable a better understanding of the turnover dynamics of non-native species in fragmented landscapes and will provide important information to aid in the conservation of fragmented natural areas impacted by the spread and establishment of non-native species in currently threatened ecosystems.

Material and methods

Study site and data collection

Arthropods were sampled using nine 50m x 50m plots located in four native fragments of pristine forest on Terceira Island in the Azores. The plots were setup within the ISLANBIODIV project (Borges et al. 2017; Cicconardi et al. 2017). Arthropods were sampled using a passive flight interception trap called a SLAM (Sea, Land, and Air Malaise) trap. The collecting bottles were collected and changed every three months; thus, each sample covers one season of the year. For the current study, we used data sampled over the years 2012 –2016 (inclusive). The arthropods were grouped by their native and non-native colonisation strategies. A more comprehensive outline of the study site (including a map) and the sampling methodology is provided in Appendix S1 in the Supporting Information (see also Borges et al. 2017).

For the climatic data, we used data from the CIELO Model (Azevedo et al. 1999). The CIELO model is a simple parcel model, based on the transformations experienced by an air mass ascending a mountain, which simulates the evolution of an air parcel's physical properties, starting from the sea level. Two Principal Components Analysis (PCA) axes were calculated using the climatic variables mean annual temperature, annual rainfall and relative humidity. The PCA was undertaken using the '*vegan*' R package (Oksanen et al. 2013), and we took the first two axes as they explained ~ 99% of the variance. The first axis (P1) corresponded to differences in temperature and precipitation, whilst the second axis (P2) corresponded more to differences in humidity. In addition, we used an 'index of Disturbance' developed by Cardoso et al. (2013) for the Azores that models disturbance by considering landscape configuration and proximity of human-modified habitat to each patch of pristine native forest (see Appendix S1). We also calculated the elevation of each plot using a digital elevation model (DEM) for Terceira Island.

We pooled the samples within each year to create yearly datasets for each of the nine plots. Where the same species had been sampled in multiple samples within a single year we combined records and summed the abundances. We then converted these data into presence-absence matrices, such that for each of the nine plots we had five presence-absence matrices, one for each of the five sampling years (2012–2016).

Calculating temporal beta-diversity: Prediction 1

To examine whether temporal beta-diversity was greater for non-natives than for natives (Prediction 1), we used both pairwise and multiple-time temporal beta-diversity frameworks. First, for each plot we constructed a presence-absence matrix for the pooled 2013 samples

(the first full year of sampling, see Appendix S1) and the pooled 2016 samples. We then used the '*beta.temp'* function in the 'betapart' R package (Baselga et al. 2017) to calculate partitioned pairwise temporal beta-diversity (Sorensen index) between these two years, and we stored both partition values (i.e. temporal turnover and temporal nestedness-dissimilarity) as well as the overall Sorensen's dissimilarity value. This analysis was undertaken separately for native and non-native species. To determine whether the observed pairwise temporal beta-diversity and partition values were significantly different from random expectation, we followed Baselga et al. (2015) and used an FE null model (Ulrich and Gotelli 2007) whereby row (site species richness) marginal totals were allowed to vary and column (species incidences) marginal totals are fixed. In this context, the FE null model characterises a situation whereby species randomly colonise and go extinct at sites, from a common regional pool (Baselga et al. 2015). This null model was implemented using the 'c0' algorithm in the 'vegan' R package (Oksanen et al. 2013). This null model was used to randomise the 2016 presence/absence matrix, which was then compared to the empirical 2013 presence/absence matrix, using the '*beta.temp'* function. This process was repeated 1000 times, for both the native and the non-native species data; the overall dissimilarity value, and the two partition values, was stored in each instance. Using these null model values, we calculated the Z-scores for the six metrics (the three temporal beta-diversity metrics, for both the native and non-native presence/absence matrices). A two-sided *P*-value was also calculated for each Z-score. To ensure that our results were consistent across the two main beta-diversity partitioning frameworks, we also calculated temporal beta-diversity and re-ran the above analyses using the Carvalho partitioning framework (Carvalho et al. 2012), the Sorensen family of beta-diversity metrics and the BAT R package (Cardoso et al. 2014). The Carvalho partitioning framework differs from the Baselga framework in that it partitions overall beta-diversity into turnover and richness difference components, instead of turnover and nestedness-dissimilarity components.

Spatial beta-diversity studies have shown that pairwise beta-diversity metrics and multisite beta-diversity metrics (i.e. spatial beta-diversity aggregated across multiple sites) can reveal different patterns (Baselga 2013). Thus, we adapted the *'beta.temp'* function to calculate partitioned multiple-time dissimilarity, again based on the Sorensen index. This is an aggregate measure that enables the calculation of temporal beta-diversity across multiple time periods for the same site. We calculated multiple-time dissimilarity for both native and non-

native species for four years (2013 – 2016) and compared the resultant beta-diversity values with their pairwise counterparts.

Calculating turnover: Prediction 2

Following Burns (2015), turnover was calculated as the total number of colonisation and extinction events across the five years (2012 – 2016). That is, colonisation was considered to have occurred if a species was not present in a plot in year *i*, but was present in year *i+1*. Equally, under this turnover framework, an extinction event was considered to have occurred if a species was present in a plot in year *i*, but not in year *i+1*.

To test Prediction 2 (that colonisation rate will be greater than extinction rate for non-native species, but equivalent to extinction rate for native species), we calculated the number of turnover events for each individual species, across all nine plots. Reduced major axis regression was then used to determine how colonisation rate varied with extinction rate (see Burns 2015) as both variables (colonisation and extinction rate) contained random error; in such cases, standard linear regression underestimates the slope of the relationship. The regression models were calculated using the 'lmodel2' R package (Legendre 2014), and we used the standard major axis (SMA) method. Models were fitted for native and non-native species separately. In this analysis, a slope significantly greater than one, or an intercept significantly greater than zero, would indicate that the colonisation rate exceeded extinction rate (for either native or non-native species) and thus that the number of native/non-native species increased in the fragments over the five years, and *vice versa.*

Explaining variation in temporal beta-diversity

To determine whether any of our environmental variables explained variation in the turnover component of temporal beta-diversity, we undertook a model comparison approach using generalised linear models (GLMs). We used GLMs with the Gaussian family in these analyses, and normality of the response variables was assessed using the Shapiro-Wilks test (in both cases the null hypothesis that the response variable was normally distributed could not be rejected). We ran the model comparison twice, once for each of two response variables: 1) the pairwise temporal turnover beta-diversity partition values of native species, and 2) the pairwise temporal turnover beta-diversity partition values of non-native species. As predictor variables, we started with elevation (log transformed), disturbance (log transformed) and two climatic PCA axes (P1 and P2). All predictors were standardised to have a mean of 0 and standard deviation of 1 to enable comparison of the effect sizes.

Multicollinearity was assessed using variance inflation factors (VIFs), which resulted in P1 being removed from all subsequent analyses as it was very highly correlated with altitude. The three remaining predictor variables (elevation, disturbance and P2) all had VIFs under ten.

Using these response and predictor variables, we compared a full set of generalised linear models (GLMs) within an information theoretic approach (Burnham and Anderson 2002). For each response variable, a full set of models were compared using Akaike's information criterion corrected for small sample size (AIC_c; see Burnham and Anderson 2002). The model with the lowest AIC_c was considered the best model, whilst all models with $\Delta AIC_c <= 2$ were considered to have similar support. As our data were sampled using 50 m x 50 m quadrats nested within fragments, we used a spatial autocovariate within an auto-Gaussian regression approach to account for the experimental design. First, for each response variable, we fitted the global model and extracted the residuals. We then created a spatial autocovariate using the residuals (see Crase et al. 2012) and the 'autocov_dist' function in the 'spdep' R package (Bivand 2017). The neighbourhood radius was set to encompass all plots, and we used the 'inverse' type and row standardised (W) style settings. The spatial autocovariate was fixed in the model selection. For all models with $\Delta AIC_c <= 2$, we also checked the residuals for homoscedasticity, and we checked for any remaining spatial autocorrelation in the residuals using the 'spdep' R package (Bivand 2017), the '*nb2listw*' function and row standardised weights. We also re-ran the model selection analyses using Gaussian mixed effect models with 'fragment' as a random effect (random intercept); however, the variance of the random effect was very close to zero in both cases and these results are not discussed further.

Sensitivity analyses

We ran two sensitivity analyses to ensure our results were robust. First, to ensure our sampling was sufficient we calculated sampling completeness estimates for each year in each plot using the iNEXT R package (Hill number order q = 0, Hsieh et al. 2016). Second, we set up a tenth plot in which we placed three SLAM traps instead of one to determine whether the use of a single SLAM trap in each of the plots was sufficient to capture the relevant community properties. A full methodology for each of the sensitivity analyses is provided in Appendix S1. All analyses were undertaken using R (version 3.4.3, R Core Team 2017).

Results

Dataset summary

Over the five years, we sampled 28,704 arthropod specimens, representing 147 species and morpho species (no. of native sp. = 89 and no. of non-native sp. = 58), across ten plots (nine plots were used in the main analysis and a tenth plot was used in the sensitivity tests). Across the nine plots that formed the main basis of this study, the mean richness (i.e. mean of each plot across the five years) of species in a plot ranged from 21 to 38 and 3 to 11, for native and non-native species respectively (Table 1). Mean total abundance (i.e. abundance of all species in a plot) ranged from 205 to 886 and 4 to 68 for native and non-native species respectively (Table 1).

Temporal beta-diversity

For all nine plots, overall temporal beta-diversity was larger for non-native species than for native species (Table 2; Fig. 1), confirming Prediction 1. The temporal turnover component of overall pairwise beta-diversity was larger than the temporal nestedness-dissimilarity component for all but one plot for non-native species, and for five of the nine plots for native species (Fig. 1). For overall temporal beta-diversity, the Z-scores were negative for all but one plot for native species, whilst Z-scores were both positive and negative for non-native species (Table 2). Four of the overall pairwise beta Z-scores for native species were significant, whilst only one of the overall pairwise beta Z-scores for non-native species was significant (Table 2). The null model results for the pairwise temporal beta-diversity partitions were similar to the results for the overall pairwise temporal beta-diversity values (see Table 2). This outcome did not change when the Carvalho pairwise beta-diversity partitioning framework was used rather than the Baselga approach (see Appendix S2): overall pairwise beta-diversity and the two partitions were all positively and significantly correlated between the two approaches (all Pearson's correlation coefficients > 0.90, and all *P*-values < 0.001), and the same overall picture emerged regardless of the approach used (compare Fig. 1 with Fig. S3 in Appendix S2).

Using multiple-time dissimilarity produced similar results to the pairwise temporal beta-diversity analysis (see Figure S4 in Appendix S3): overall temporal beta-diversity was larger for non-native species than for native species, for all nine plots, and on average the temporal nestedness-dissimilarity component represented a larger proportion of total temporal beta-diversity for native species than for non-native species. One interesting difference was non-native species in Plot 6 (compare Fig.1 with Fig.S4), whereby the pairwise measure indicated

that the nestedness-dissimilarity component represented 100% of overall beta-diversity, but only 16% using multiple-time dissimilarity.

Differences in colonisation and extinction rates

Reduced major axis regression of the number of colonisation events against the number of extinction events revealed that, contrary to Prediction 2, the slope of the relationship was significantly greater than one for both native (slope = 1.26; 95% CI = 1.11 – 1.44) and non-native species (slope = 1.28; 95% CI = 1.16 – 1.42) (Fig. 2), indicating that the colonisation rate exceeded the extinction rate for both groups. The intercept of the relationship was not significantly different from zero for either native (intercept = 0.17; 95% CI = -0.22 – 0.51) or non-native (intercept = -0.11; 95% CI = -0.38 – 0.13) species. The R^2 values for both regression models were: 0.64 and 0.86 for the native and non-native species models, respectively.

Explaining variation in temporal beta-diversity between plots

When the turnover partition (of overall pairwise temporal beta-diversity) values were used as the response variables in a set of GLMs, the selection procedure indicated that the only predictor variable in both the best native and non-native species models was the fixed spatial autocovariate, and there were no additional models within 2 ΔAIC_c of either best model. Re-running the model selection using the turnover component of multiple-time dissimilarity produced the same overall results.

Sensitivity analyses

Sample completeness estimates indicated that our sampling was sufficient: the mean sample completeness estimate across all years and plots was 0.97 (range = 0.81 to 1.00, the results for each year and plot are presented in Table S2 in Appendix S4). Using three SLAM traps in a plot rather than one did not result in substantially different sampled communities according to various measures of diversity (see Appendix S4).

Discussion

We have undertaken an evaluation of the differences in temporal beta-diversity patterns between native and non-native arthropod species across nine native forest plots in the Azores for which a time series of five years is available (2012 - 2016).

Non-native species have larger rates of temporal beta-diversity than native species in Azorean forest fragments

The results of our temporal beta-diversity analyses (both pairwise and multiple-time dissimilarity) indicated that, in accordance with Prediction 1, temporal beta-diversity was considerably greater for non-native species than for native species, across all nine plots. In addition, with one exception (Plot 6 when using pairwise beta-diversity, Fig. 1), for non-native species the largest component of temporal beta-diversity was by far the temporal turnover partition, indicating an actual turnover of species rather than nested patterns in richness (Baselga partition) or richness differences (Carvalho partition) between years.

Burns (2015), in his theory of island biogeography for exotic species (TIBE), attributed differences in turnover rates between natives and non-natives to standard island biogeographical variables. However, Burns was focused on true islands. In our study system of habitat islands, we found that, in regard to overall pairwise temporal beta-diversity for non-native species, the null model analyses were only significant in one case, and the signs of the Z-scores varied between the plots (Table 2). These findings, in combination with previous work in our study system (e.g. Borges et al. 2006, 2008, Florencio et al. 2016), appear to support the notion that the distribution of non-native arthropods in Azorean native forests is driven by stochastic processes and occupancy dynamics, possibly due to source-sink processes (see also Borges et al. 2008). In a study of temporal beta-diversity patterns of birds in France, Baselga et al. (2015, p.9) also found that temporal changes in assemblages were not significantly different from a null model and concluded that "the observed changes in species composition of local bird assemblages might be the consequence of stochastic processes in which species populations appeared and disappeared from specific localities in a random-like way."

Many non-native arthropod species in the Azores are adapted to human land-uses (Borges et al. 2008, Rigal et al. 2018), and thus we would expect there be a large number, and thus high potential for mass effects (Shmida and Wilson 1985), of non-natives in the disturbed landscapes surrounding the fragments (see also Borges et al. 2006). The Azores has undergone substantial land use change since human colonisation of the archipelago (Triantis et al. 2010), and native forest fragments in the Azores are characterised by hard boundaries, i.e. there is an abrupt change from native forest habitat to anthropogenic habitat (Borges et al. 2006, 2008). As such, there are likely to be large mass effects and a constant supply of non-

native individuals permeating into the native forest where they frequently undergo local extinction and re-colonisation, leading to high beta-diversity through time. Thus, it seems likely that is not just the size of the native habitat that underpins the colonisation rate of non-natives (as in true islands cf. Burns 2015) but also the amount of surrounding anthropogenic habitat and size of the non-native source pool, which is known to be large in the Azores (Borges et al. 2010). More detailed studies focusing on the habitat affinities and dispersal ecology of non-native species are needed to further explore this possibility. Interestingly, our disturbance metric, that incorporates surrounding land use, was not an important predictor of non-native temporal beta-diversity in the linear model selection analysis. However, as all of the native forest fragments on Terceira are surrounded by human land uses, it is likely that there was simply not enough variation in the disturbance metric between plots.

In regards to the processes underpinning temporal beta-diversity patterns of native species, the results are more equivocal. Overall pairwise temporal beta-diversity was significantly lower than expected by chance in four of the nine plots for native species, in comparison to only one of the nine plots for non-native species. This indicates a stronger role for deterministic processes driving temporal beta-diversity and turnover in native species assemblages (Baselga et al. 2015). However, as with non-native species, none of our predictor variables were found to explain variation in the temporal beta-diversity of native species. The reasons for this finding are unclear but could simply be due to the fact that our experimental design did not allow us to test for the importance of other biogeographic variables such as area on turnover (MacArthur & Wilson 1967). Further studies examining the turnover dynamics of native and non-native species in habitat fragments are needed.

Colonization and extinction rates for native and non-native species

Our Prediction 2, that colonisation rate will be greater than extinction rate for non-native species, whilst colonisation rate will be roughly equivalent to extinction rate for native species, was not borne out by the data. Whilst we observed that the colonisation rate was greater than the extinction rate for non-natives, contrary to expectations we found a similar pattern for native species (Fig. 2). Whilst this finding is expected for non-native species, these results could imply either that many of the native species in the fragments have high dispersal ability and are easily able to disperse between plots and fragments, or possibly that native species have not yet reached equilibrium following substantial habitat loss over the last few centuries. An alternative explanation is that our sampling did not accurately record all

colonisation and extinction events during the study period. Previous work on turnover on islands has shown that the calculation of turnover rate is sensitive to the grain size of the time series data analysed (e.g. were samples carried out every year or every ten years) (e.g. Russell et al. 1995, Whittaker et al. 2000). Considering these issues, inevitably we have not recorded every true turnover event (i.e. crypto-turnover), and equally, due to sampling error, we have likely missed individuals in certain instances and thus erroneously recorded turnover events (i.e. pseudo-turnover). However, sampling was every three months (as opposed to multiple years in most island studies), and thus a species had to be absent across all the monthly samples for an extinction event to be classified. We also carried out sensitivity analyses to ensure our sampling effort was sufficient. As a result, we are confident that our sampling protocol has generated data of sufficient quality to test our predictions.

Implications for conservation and biodiversity management

Non-native species are thought to be leading drivers of contemporary species extinctions, and the issue seems particularly acute in true and habitat island systems (Sax and Gaines 2003, Cardoso et al. 2010, Bellard et al. 2016). However, the biogeography of non-native species is not well known. Specifically, it is not known whether standard biogeographical theory and metrics derived from the study of native species can be accurately applied to non-native taxa. As a result of this uncertainty, a number of recent studies have focused on examining the differences and similarities between natives and non-natives using classic biogeographical and ecological patterns, such as the ISAR and the abundance-occupancy relationship (e.g. Blackburn et al. 2008, Rigal et al. 2013, Burns 2015). The results of our study contribute towards filling this knowledge gap by showing that it cannot be assumed *a priori* that native and non-native taxa within the same community are similarly assembled and will follow the same temporal dynamics.

Importantly, our results indicate that it might not be possible to apply simple biogeographical principles (e.g. Wilson and Willis 1975) when devising non-native species management plans in fragmented landscapes. Rather, management should be based on the results of biogeographical and ecological studies explicitly focused on non-native taxa. A corollary of this statement is that there is an urgent need for additional studies focused on outlining and testing biogeographical theory in the context of non-native species (Patiño et al. 2017). In the native forest sampled in our study, the high rate of stochastic turnover of non-native species that we observed indicates that attempts to simply reduce the populations of non-native

species *in situ* within native habitats may not be successful. This is because for many non-native species the native habitat is likely just a sink, and the constant immigration of individuals from anthropogenic source habitats in close proximity to the native habitats (i.e. mass effects) means local extinction of non-natives within the native forest is unlikely to be permanent. Thus, a more efficient future management strategy and land-use policy will be to interrupt these source-sink dynamics by improving the harsh boundaries between native habitat and adjacent anthropogenic habitat, and in the longer term to design and create a more graded landscape mosaic (Lindenmayer and Fischer 2006) whereby contrasting land uses are not simply knitted together in an ad hoc fashion. The high turnover of non-native species also brings into question the ability of non-natives to, amongst other things, replace the functional roles of extirpated native species (see Whittaker et al. 2014; Rigal et al. 2018) or increase functional redundancy in fragmented landscapes. Functional diversity studies that focus on non-native species are often based on static time periods (e.g. a sample from one year) and their conclusions thus do not account for the fact that many non-native species present in a patch may simply be ephemeral members of a given community.

Acknowledgements **-** Andrés Baselga kindly answered questions related to the calculation and interpretation of beta-diversity. Rob Whittaker, François Rigal and three anonymous reviewers provided helpful comments on an earlier version of the manuscript. A large number of students financed by the EU Programs ERASMUS and EURODYSSÉE sorted the samples prior to species assignment by one of us (PB), and we are grateful to all of them: Adal Humberto Díaz Raya, Alejandra Ros Prieto, David Rodilla Rivas, Daniel Ehrhart, Juan Ignacio Pitarch Peréz, Juan Manuel Taboada Alvarez, Helena Marugán Páramo, Laura Cáceres Sabater, Laura Gallardo, Marija Tomašić, Óscar García Contreras, Percy de Laminne de Bex, Ruben Murillo Garcia, Sergio Fernandez, Sophie Wallon, and William Razey. This manuscript was also partly financed by Portuguese National Funds, through FCT – Fundação para a Ciência e a Tecnologia, within the project UID/BIA/00329/2013 and Portuguese FCT-NETBIOME –ISLANDBIODIV grant 0003/2011. The Natural Park of Terceira (Azores) provided the necessary authorization for sampling.

Author contributions – TM designed the analytical study. PB designed the sampling methodology and collected the data with RC and RN. TM analyzed the data. TM wrote the manuscript, with the help of JS and PB.

References

Anderson, M. J. et al. 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. — Ecology Letters 14: 19-28.

Azevedo, E. B. d. et al. 1999. Modelling the local climate in island environments: water balance applications. — Agric. Water Manag. 40: 393-403.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. — — Global Ecol. Biogeogr. 19: 134-143.

Baselga, A. 2013. Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. — Ecography 36: 124-128.

Baselga, A. et al. 2015. Temporal beta diversity of bird assemblages in agricultural landscapes: land cover change vs. stochastic processes. — PLoS One 10: e0127913.

Baselga, A. et al. 2017. betapart: partitioning beta diversity into turnover and nestedness components. R Package.

Bellard, C. et al. 2016. Alien species as a driver of recent extinctions. — Biol. Lett. 12: 20150623.

Bivand, R. 2017. spdep: spatial dependence: weighting schemes, statistics and models. R Package.

Blackburn, T. M. et al. 2004. Avian extinction and mammalian introductions on oceanic islands. — Science 305: 1955-1958.

Blackburn, T. M. et al. 2008. The island biogeography of exotic bird species. — Global Ecol. Biogeogr. 17: 246-251.

Blackburn, T. M. et al. 2016. On the island biogeography of aliens: a global analysis of the richness of plant and bird species on oceanic islands. — Global Ecol. Biogeogr. 25: 859-868.

Borges, P. A. V. et al. 2006. Invasibility and species richness of island endemic arthropods: a general model of endemic vs. exotic species. — J. Biogeogr. 33: 169-187.

Borges, P. A. V. et al. 2017. Seasonal dynamics of arthropods in the humid native forests of Terceira Island (Azores). — Arquipelago Life and Marine Sciences 34: 105-122.

Borges, P. A. V. et al. 2008. Insect and spider rarity in an oceanic island (Terceira, Azores): true rare and pseudo-rare species. — In: Fattorini, S. (ed), Insect Ecology and Conservation. Research Signpost, pp. 47-70.

Borges, P. A. V. et al. 2010. List of arthropods (Arthropoda). — In: Borges, P. A. V. et al. (eds), A list of the terrestrial and marine biota from the Azores. Princípia, pp. 179-246.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multi-model inference: a practical information-theoretic approach. — Springer.

Burns, K. C. 2015. A theory of island biogeography for exotic species. — Am. Nat. 186: 441-451.

Cardoso, P. et al. 2010. Drivers of diversity in Macaronesian spiders and the role of species extinctions. — J. Biogeogr. 37: 1034-1046.

Cardoso, P. et al. 2014. BAT - Biodiversity Assessment Tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. — Methods Ecol. Evol. 6: 232-236.

Cardoso, P. et al. 2013. Integrating landscape disturbance and indicator species in conservation studies. — PLoS One 8: e63294.

Carvalho, J. C. et al. 2012. Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. — Global Ecol. Biogeogr. 21: 760-771.

Cicconardi, F. et al. 2017. MtDNA metagenomics reveals large-scale invasion of belowground arthropod communities by introduced species. — Mol. Ecol. 26: 3104-3115.

Clavero, M. and García-Berthou, E. 2005. Invasive species are a leading cause of animal extinctions. — Trends Ecol. Evol. 20: 110.

Crase, B. et al. 2012. A new method for dealing with residual spatial autocorrelation in species distribution models. — Ecography 35: 879-888.

Didham, R. K. et al. 2007. Interactive effects of habitat modification and species invasion on native species decline. — Trends Ecol. Evol. 22: 489-496.

Dyer, E. E. et al. 2017. The global distribution and drivers of alien bird species richness. — PLoS Biol. 15: e2000942.

Ferger, S. W. et al. 2017. Synergistic effects of climate and land use on avian beta-diversity. — Div Distrib. 23: 1246-1255.

Florencio, M. et al. 2016. The role of plant fidelity and land-use changes on island exotic and indigenous canopy spiders at local and regional scales. — Biol. Invas. 18: 2309-2324.

Hsieh, T. C. et al. 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). — Methods Ecol. Evol. 7: 1451-1456.

Karp, D. S. et al. 2018. Agriculture erases climate-driven β-diversity in Neotropical bird communities. — Glob. Change Biol. 24: 338-349.

Legendre, P. 2014. lmodel2: model II regression. R package.

Lindenmayer, D. B. and Fischer, J. 2006. Habitat fragmentation and landscape change: an ecological and conservation synthesis. — Island Press.

MacArthur, R. H. and Wilson, E. O. 1967. The theory of island biogeography. — Princeton University Press.

Matthews, T. J. 2015. Analysing and modelling the impact of habitat fragmentation on species diversity: a macroecological perspective. — Front. Biogeogr. 7: 60-68.

McKinney, M.L. and Lockwood, J.L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. — Trends Ecol. Evol. 14: 450–453.

524 Mooney, H. A. and Hobbs, R. J. (eds.) 2000. Invasive species in a changing world. — Island
525 Press.

526 Oksanen, J. F. et al. 2013. "Package 'vegan'. R package version 2.0-9.

527 Patiño, J. et al. 2017. A roadmap for island biology: 50 fundamental questions after 50 years
528 of The Theory of Island Biogeography. — J. Biogeogr. 44: 963-983.

529 Pyšek, P. 1998. Alien and native species in Central European urban floras: a quantitative
530 comparison. — J. Biogeogr. 25: 155-163.

531 R Core Team 2017. R: A language and environment for statistical computing. R foundation
532 for statistical computing.

533 Rigal, F. et al. 2013. Integration of non-indigenous species within the interspecific
534 abundance-occupancy relationship. — Acta Oecol. 48: 69-75.

535 Rigal, F. et al. 2018. Functional traits of indigenous and exotic ground-dwelling arthropods
536 show contrasting responses to land-use changes in an oceanic island, Terceira, Azores.
537 Div. Distrib. 24: 36-47.

538 Russell, G. J. et al. 1995. A century of turnover: community dynamics at three timescales. —
539 J. Animal Ecol. 64: 628-641.

540 Sax, D. F. and Gaines, S. D. 2003. Species diversity: from global decreases to local increases.
541 — Trends Ecol. Evol. 18: 561-566.

542 Sax, D. F. et al. 2002. Species invasions exceed extinctions on islands worldwide: a
543 comparative study of plants and birds. — Am. Nat. 160: 766-783.

544 Seebens, H. et al. 2017. No saturation in the accumulation of alien species worldwide. —
545 Nat. Commun. 8: 14435.

546 Sgarbi, L. F. and Melo, A. S. 2017. You don't belong here: explaining the excess of rare
547 species in terms of habitat, space and time. — Oikos DOI: 10.1111/oik.04855

548 Shmida, A. and Wilson, M. V. 1985. Biological determinants of species diversity. — J.
549 Biogeogr. 12: 1-20.

550 Tonkin, J. D. et al. 2017. Seasonality and predictability shape temporal species diversity. —
551 Ecology 98: 1201–1216

552 Triantis, K. A. et al. 2010. Extinction debt on oceanic islands. — Ecography 33: 285-294.

553 Ulrich, W. and Gotelli, N. J. 2007. Null model analysis of species nestedness patterns. —
554 Ecology 88: 1824-1831.

555 Whittaker, R. J. and Fernández-Palacios, J. M. 2007. Island biogeography: ecology,
556 evolution, and conservation. — Oxford University Press.

557 Whittaker, R. J. et al. 2000. How to go extinct: lessons from the lost plants of Krakatau. — J.
558 Biogeogr. 27: 1049-1064.

559 Whittaker, R. J. et al. 2014. Functional biogeography of oceanic islands and the scaling of
560 functional diversity in the Azores. — Proc. Natl Acad. Sci. USA 111: 13709–13714.

Williamson, M. 1996. Biological invasions. — Chapman & Hall.

Wilson, E. O. and Willis, E. O. 1975. Applied biogeography. — In: Cody, M. L. and Diamond, J. M. (eds), Ecology and evolution of communities Harvard University Press, pp. 522-534.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Additional methodological information, including plot locations and environmental data.

Appendix S2. Pairwise beta-diversity results using the Carvalho partition framework

Appendix S3. Multiple-time dissimilarity results

Appendix S4. Sensitivity Analyses Full Results

TABLES

Table 1. The mean richness (M. Richness), mean abundance (M. Abundance), and the number of colonisation (Colonis.), extinction, and total turnover events of arthropod species across nine native forest plots on Terceira Island, in the Azores. For each plot, the data are provided for native (Nat) and non-native (Non) species separately. Each plot was sampled multiple times across five years and samples were pooled to create five yearly samples (2012 – 2016). An extinction event was deemed to have occurred if a species was present in year *i* but not in year *i+1*, and *vice versa* for a colonisation event (Plot notation as in Table S1 and Figure S1).

Plot	Type	M. Richness	M. Abundance	Colonis.	Extinction	Turnover
1	Nat	32.8	790.8	27	24	51
2	Nat	30.2	496.4	28	26	54
3	Nat	25.6	558.0	19	20	39
4	Nat	38.0	885.6	46	20	66
5	Nat	25.0	511.0	36	17	53
6	Nat	21.0	204.6	26	26	52
7	Nat	25.0	272.8	28	21	49
8	Nat	20.6	480.2	21	16	37
9	Nat	30.2	489.4	27	22	49
1	Non	6.8	20.8	17	10	27
2	Non	4.6	9.4	10	11	21
3	Non	4.0	5.6	10	9	19
4	Non	10.8	67.6	31	21	52
5	Non	4.25	11.2	10	8	18
6	Non	3.75	4.4	13	12	25
7	Non	3.2	5.0	8	7	15

8	Non	4.4	8.8	19	14	33
9	Non	5.0	18.2	13	15	28

584

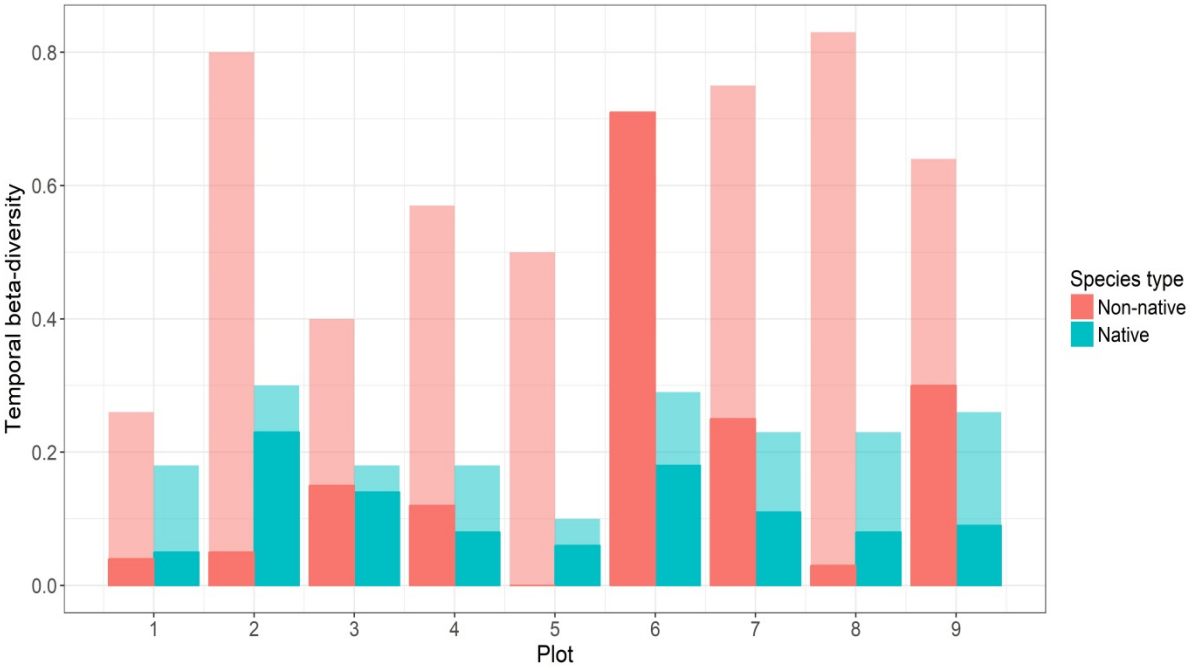
585

586

Table 2. Pairwise temporal beta-diversity values for arthropod species sampled in 2013 and 2016 in nine native forest plots on Terceira Island, in the Azores. For each plot, the data are provided for native (Nat) and non-native (Non) species separately. Overall temporal beta-diversity values (Sorensen dissimilarity index) are provided in addition to the temporal turnover (Turn.) and temporal nestedness-dissimilarity (Nest.) components of overall temporal beta-diversity. For the two partition values and the overall temporal beta-diversity value, significance was determined using an FE null model (1000 iterations). For each of the three beta-diversity values, the Z-score (Z) and associated *P*-value (*P*) are provided (see 'Materials and methods'). *P*-values significant at the 0.05 level are highlighted in bold (Plot notation as in Table S1 and Figure S1). The overall temporal beta-diversity differ very slightly from the sum of the turnover and nestedness components in certain plots due to rounding error.

Plot	Type	Temporal beta-diversity			Turnover		Nestedness		Overall	
		Turn.	Nest.	Overall	Z	*P*	Z	*P*	Z	*P*
1	Nat	0.12	0.05	0.18	-0.94	0.35	-1.48	0.14	-2.49	**0.01**
2	Nat	0.08	0.23	0.30	-0.85	0.39	0.52	0.60	-0.33	0.74
3	Nat	0.05	0.14	0.18	-2.92	**<0.01**	3.64	**<0.01**	-1.08	0.28
4	Nat	0.11	0.08	0.18	-0.36	0.72	-1.58	0.11	-1.96	**0.04**
5	Nat	0.04	0.06	0.10	-2.04	**0.04**	-0.24	0.81	-2.53	**0.01**
6	Nat	0.11	0.18	0.29	-2.68	**0.01**	6.17	**<0.01**	-0.1	0.92
7	Nat	0.12	0.11	0.23	-1.00	0.32	0.75	0.45	-0.44	0.66
8	Nat	0.15	0.08	0.23	-3.45	**<0.01**	1.22	0.22	-3.48	**<0.01**
9	Nat	0.17	0.09	0.26	0.11	0.91	-0.72	0.47	-0.59	0.56
1	Non	0.22	0.04	0.26	-1.13	0.26	-0.94	0.35	-2.58	**0.01**
2	Non	0.75	0.05	0.80	1.50	0.13	-0.39	0.70	1.63	0.10
3	Non	0.25	0.15	0.40	-1.52	0.13	0.74	0.46	-1.48	0.14
4	Non	0.44	0.12	0.57	-0.24	0.81	-0.27	0.79	-0.63	0.53
5	Non	0.5	0.00	0.50	0.75	0.45	-1.72	0.08	-0.47	0.64
6	Non	0.00	0.71	0.71	-4.84	**<0.01**	11.20	**<0.01**	-0.72	0.47
7	Non	0.5	0.25	0.75	-0.38	0.70	1.73	0.08	0.69	0.49
8	Non	0.8	0.03	0.83	0.02	0.98	0.06	0.95	0.05	0.96
9	Non	0.33	0.3	0.64	-1.06	0.29	1.63	0.10	-0.09	0.92

602 **FIGURES**



603

604

Figure 1. Pairwise temporal beta-diversity values for native and non-native arthropod species across nine plots of native forest on Terceira Island, in the Azores. For each plot, temporal beta-diversity was calculated using the pooled 2013 samples and the pooled 2016 samples. For each plot, temporal beta-diversity was calculated separately for native species (blue bars) and non-native species (red bars). The height of each bar corresponds to the overall temporal beta-diversity. Overall temporal beta was also partitioned into nestedness and turnover components using the Baselga partition approach (Baselga et al. 2017). Within each bar, the dark shaded area rising from the x-axis corresponds to the nestedness component of overall temporal beta diversity. Thus, the lighter shaded area within each bar that rises from the dark shaded area corresponds to the turnover component.

605

606

607

608

609

610

611

612

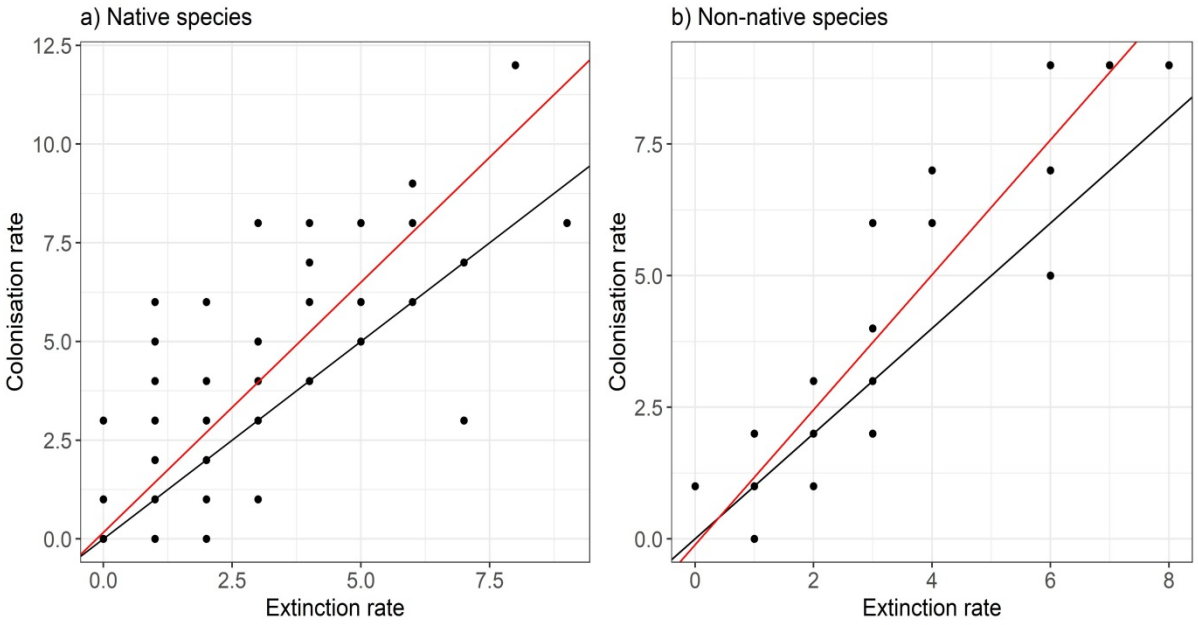


Figure 2. The relationship between the number of colonisation events and the number of extinction events in native (a) and non-native (b) arthropod species sampled in nine native forest plots on Terceira Island in the Azores. Each plot was sampled multiple times across five years and samples were pooled to create five yearly samples. Turnover was then calculated as the total number of colonisation and extinction events across the five years (see 'Materials and methods'). In (a) and (b), the black line is the isometric line (i.e. intercept of zero and slope of 1) and the red line is the best fit line from reduced major axis regression. In both cases the best fit regression line is significantly greater than one.

SUPPORTING INFORMATION

Differential temporal beta-diversity patterns of native and non-native arthropod species in a fragmented native forest landscape

Thomas J. Matthews, Jon Sadler, Rui Carvalho, Rui Nunes, Paulo A. V. Borges

Appendix S1 Additional methodological information

Study site

The Azorean archipelago is located in the North Atlantic, roughly between 37º to 40º N latitude and 25º to 3º W longitude. Since human occupation of the islands, there have been substantial changes in the size and quality of native habitats, mostly due to the creation of urban areas, agriculture fields, pastures and non-native plantations (Borges et al. 2008, Triantis et al. 2010). Terceira Island (Fig. 1), a roughly circular island of 402 km^2 area, contains the largest area of native pristine forests in the Azores (Triantis et al. 2010), with five main fragments of native forest distributed across four main volcanic polygenetic complexes.

Data collection

Arthropods were sampled using nine 50m x 50m plots located in four native fragments of pristine forest on Terceira setup within the ISLANBIODIV project (Cicconardi et al. 2017): Serra de Santa Bárbara (Plots T07, T48, T49, T164), Biscoito da Ferraria (Plots T01, T02, T41), Terra Brava (Plot T15) and Galhardo (Plot T33) (see Figure S1, below). Arthropods were sampled using a passive flight interception trap called a SLAM (Sea, Land, and Air Malaise) trap. The SLAM traps are approximately 110 x 110 x 110 cm (see Fig. S2 in Appendix S1), and work by intercepting arthropods on an area of black mesh and funnelling them into a sampling bottle filled with a killing liquid. Propylene-glycol was used as it persists for a long time without evaporating, and enables the collection of good quality specimens for posterior DNA extraction. The collecting bottles were collected and changed every three months; thus, each sample covers one season of the year. However, due to logistical challenges and problems with the traps, in a very small number of cases (see Table S1 in Appendix S1) certain three-month samples were excluded. Further details on the method can be found in Borges et al. (2017). Samples were sorted and individuals identified to species level by experienced taxonomists and to morpho species where specific determinations were not possible. The arthropods were then grouped by their native and non-

native colonisation strategies. For the current study, we used data sampled over the years 2012 –2016 (inclusive). Sampling only commenced half way through 2012 (see Table S1, below) and thus for the temporal beta-diversity analyses we used 2013 as the base year to ensure that the pairwise comparisons were based on equal samples. However, for the species-level turnover analyses we used the full dataset as the missing months here are less likely to affect the results.

For the climatic data, we used the CIELO Model (Azevedo et al. 1999). The CIELO model is a simple parcel model, based on the transformations experienced by an air mass ascending a mountain, which simulates the evolution of an air parcel's physical properties, starting from the sea level. CIELO climatic data for the sites were extracted from Borges et al. (2006). In addition, we used an 'index of Disturbance' developed by Cardoso et al. (2013) for the Azores that models disturbance by considering landscape configuration and proximity of human-modified habitat to each patch of pristine native forest. Thus, in this study we represent anthropogenic disturbance of a plot by explicitly considering landscape configuration and the amount of neighboring anthropogenic habitats, ranked according to their level of intensity-use.

Species sorting and classification

Parataxonomists sorted samples to orders, and posteriorly to Recognizable Taxonomic Units (RTUs). One of the authors (PAVB) then identified to species level the RTUs of the following arthropod orders: Diplopoda (Chordeumatida, Julida), Chilopoda (Geophilomorpha, Lithobiomorpha, Scolopendromorpha), Arachnida (Araneae, Opiliones, Pseudoscorpiones) and Insecta (Blattaria, Coleoptera, Hemiptera, Microcoryphia, Neuroptera, Psocoptera, Thysanoptera, Trichoptera). All material is stored at EDTP—Entomoteca Dalberto Teixeira Pombo, University of Azores, Angra do Heroísmo, Portugal.

Arthropods were grouped into three colonization categories: endemic (i.e. restricted to the Azores); native non-endemic, i.e. species that arrived naturally to the archipelago but are present both in the Azorean Islands and elsewhere; and non-native species, i.e., species whose original distribution range did not include the Azores and that are believed to have been introduced in the Macaronesian region after human settlement in the 15th century. The non-native status was inferred either from historical records of detected species introductions or from their current distribution being closely associated with human activity. For unidentified species, if other species in the same genus, subfamily or family were present in

the archipelago and all belonged to the same colonization category (according to Borges et al. 2010), the unknown species were classified similarly. Otherwise, we assumed the species to be native. For simplicity, endemic and native non-endemic species were grouped and are termed "native" throughout the text.

Sensitivity analyses methodology

To ensure our sampling was sufficient we calculated sampling completeness estimates for each year in each plot using the iNEXT R package (Hill number order q = 0, Hsieh et al. 2016).

Due to the resources required to sample arthropods in multiple plots every three months over five years, we only placed one SLAM trap in each plot. To determine whether this was sufficient to capture the relevant properties (e.g. species composition, distribution of abundance) of the sampled communities, in 2015 we set up a tenth plot in Terra Brava (Plot T18), in which we placed three SLAM traps, spaced 30 m apart, and sampled every month. We constructed three overall assemblage matrices whereby, for each SLAM trap, the data from the 12 months of 2015 were pooled into one sample. To determine whether community composition was similar across the three traps, we calculated a number of summary statistics: 1) the number of species in each assemblage, 2) the total abundance of each assemblage, 3) the proportion of species that were sampled in all three traps (i.e. are present in all three assemblages), and 4) the distribution of abundance across the species in each assemblage. In regards to (4), we fitted the gambin species abundance distribution model, using the 'gambin' R package and a subsampling procedure to ensure sample sizes were kept consistent (see Matthews et al. 2014), to the abundances of the species in each assemblage and recorded the alpha (shape) parameter (Matthews et al. 2014). Finally, to check that spatial species turnover across the three traps was low, we calculated multisite spatial beta-diversity across the three assemblages using presence-absence data ('*beta.multi'* function; Sorensen index) and abundance data ('*beta.multi.abund'* function; Bray-Curtis multiple-site dissimilarity), using the 'betapart' R package (Baselga et al. 2017). As most species were found in all three traps, it was not possible to use a null model approach that constrained the marginal totals. All analyses were undertaken using R (version 3.4.3, R Core Team 2017).

References

Azevedo, E. B. d. et al. 1999. Modelling the local climate in island environments: water balance applications. — Agricultural Water Management 40: 393-403.

Baselga, A. et al. 2017. betapart: partitioning beta diversity into turnover and nestedness components. R Package.

Borges, P. A. V. et al. 2006. Invasibility and species richness of island endemic arthropods: a general model of endemic vs. exotic species. — Journal of Biogeography 33: 169-187.

Borges, P. A. V. et al. 2017. Seasonal dynamics of arthropods in the humid native forests of Terceira Island (Azores). — Arquipelago Life and Marine Sciences 34: 105-122.

Borges, P. A. V. et al. 2010. List of arthropods (Arthropoda). — In: Borges, P. A. V. et al. (eds), A list of the terrestrial and marine biota from the Azores. Princípia, pp. 179-246.

Cardoso, P. et al. 2013. Integrating landscape disturbance and indicator species in conservation studies. — PLOS ONE 8: e63294.

Cicconardi, F. et al. 2017. MtDNA metagenomics reveals large-scale invasion of belowground arthropod communities by introduced species. — Molecular Ecology 26: 3104-3115.

Matthews, T. J. et al. 2014. The gambin model provides a superior fit to species abundance distributions with a single free parameter: evidence, implementation and interpretation. — Ecography 37: 1002-1011.

R Core Team 2017. R: A language and environment for statistical computing. R foundation for statistical computing.

Triantis, K. A. et al. 2010. Extinction debt on oceanic islands. — Ecography 33: 285-294.

Plot locations

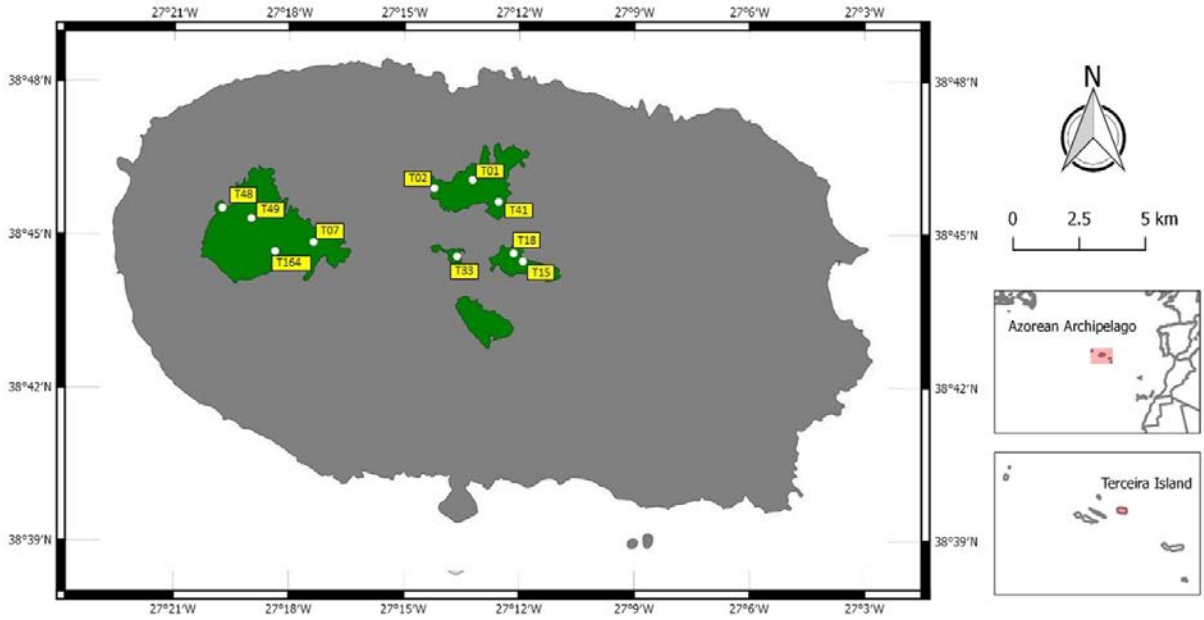


Figure S1. A map of the ten sampled 50m x 50m plots and areas of native forest on the island of Terceira, Azores.

Figure S2. Example SLAM trap in a plot within a native forest fragment on Terceira Island (Terra-Brava T18), Azores

Table S1. Sampling dates for the nine plots across the five years. A ‘1’ indicates that sampling was undertaken in this plot during this time period, whilst a ‘0’ indicates that sampling was not undertaken during this time period due to either logistical issues or problems with the traps. Codes as in Figure S1: 1- TER-NFBF-T-01; 2- TER-NFBF-T-02; 3 - TER-NFBF-TP41; 4- TER-NFPG-T-33; 5- TER-NFSB-T-07; 6- TER-NFSB-T164; 7-TER-NFSB-TE48; 8- TER-NFSB-TE49; 9- TER-NFTB-T-15,

Plot	2012 Sep.	2012 Dec.	2013 May	2013 Sep.	2013 Dec.	2014 March	2014 June	2014 Sep.	2014 Dec.
1	1	1	1	1	1	1	1	1	1
2	1	1	1	1	1	1	1	1	1
3	1	1	1	1	1	1	1	1	1
4	1	0	1	1	1	1	1	1	1
5	1	0	1	1	1	1	1	1	1
6	1	0	1	1	1	1	1	1	1
7	1	1	1	1	1	1	1	1	1
8	1	1	1	1	1	1	1	1	1
9	1	1	1	1	1	1	1	1	1

Plot	2015 March	2015 Sep.	2015 June	2015 Dec.	2016 March	2016 June	2016 Sep.	2016 Dec.
1	1	1	1	1	1	1	1	1
2	1	1	1	0	1	1	1	1
3	1	1	1	1	1	1	1	1
4	1	1	1	1	1	1	1	1
5	1	1	1	1	1	1	1	0
6	1	0	1	1	1	1	1	1
7	1	1	1	0	1	1	1	1
8	1	1	1	1	1	0	1	1
9	1	1	1	1	1	1	1	1

Appendix S2 Temporal beta-diversity results using the Carvalho et al. partition framework

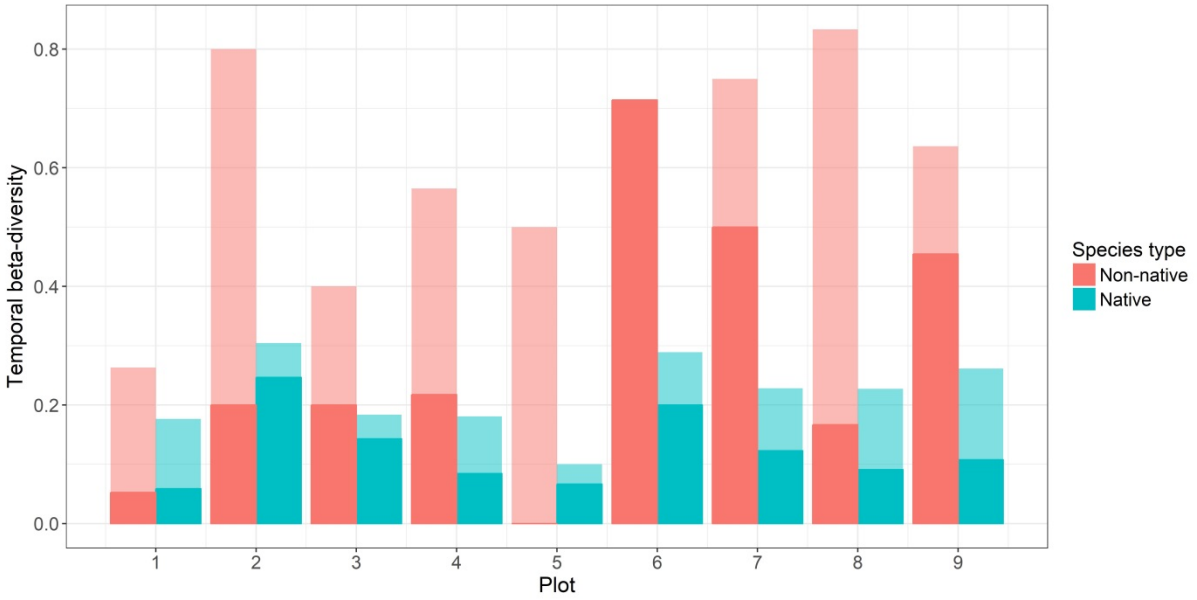


Figure S3. Pairwise temporal beta-diversity values for native and non-native arthropod species across nine plots of native forest on Terceira Island, in the Azores (Plot notation as in Table S1 and Figure S1). For each plot, temporal beta-diversity was calculated using the pooled 2013 samples and the pooled 2016 samples. For each plot, temporal beta-diversity was calculated separately for native species (blue bars) and non-native species (red bars). The height of each bar corresponds to the overall temporal beta-diversity. Overall temporal beta was also partitioned into richness differences and turnover components using the Carvalho partition approach (Carvalho et al. 2012). Within each bar, the dark shaded area rising from the x-axis corresponds to the richness differences component of overall temporal beta diversity. Thus, the lighter shaded area within each bar that rises from the dark shaded area corresponds to the turnover component.

804 **Appendix S3 Multiple-time dissimilarity results**

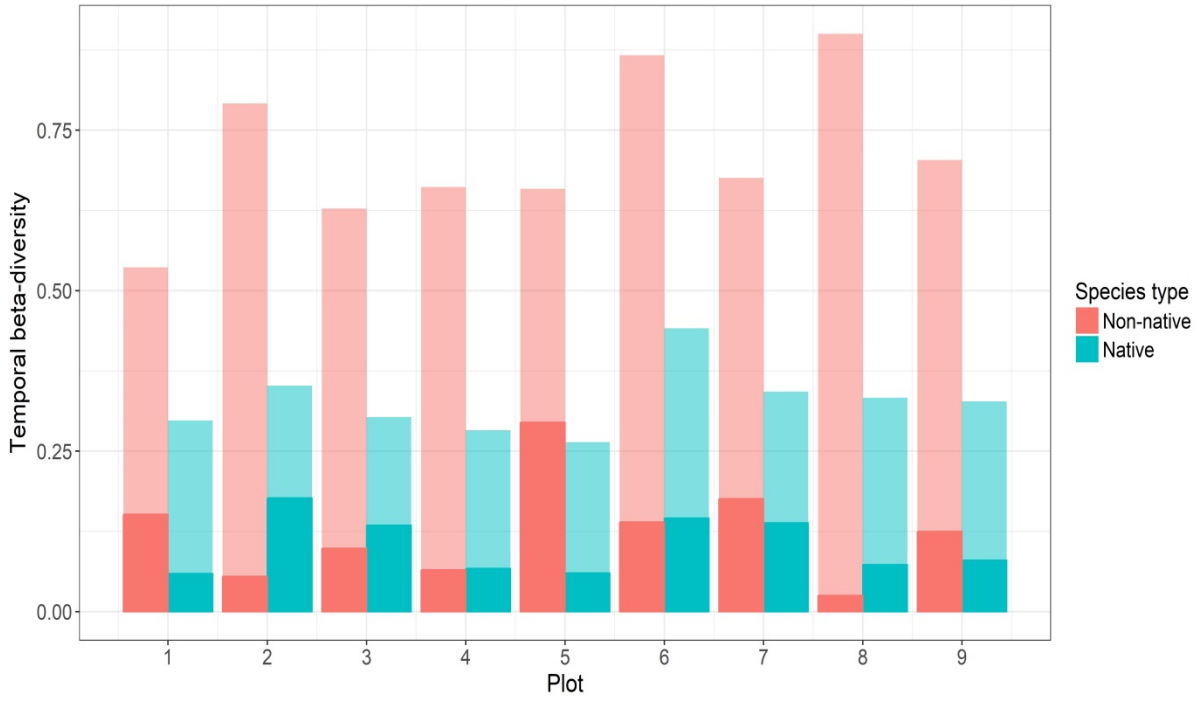


Figure S4. Multiple-time dissimilarity values for native and non-native arthropod species across nine plots of native forest on Terceira Island, in the Azores. For each plot, multiple-time dissimilarity was calculated across four years of data (2013 – 2016). For each plot, temporal beta-diversity was calculated separately for native species (blue bars) and non-native species (red bars). The height of each bar corresponds to the overall multiple-time dissimilarity was. Overall multiple-time dissimilarity was also partitioned into nestedness and turnover components using the Baselga partition approach (Baselga et al. 2017). Within each bar, the dark shaded area rising from the x-axis corresponds to the nestedness component of overall temporal beta diversity. Thus, the lighter shaded area within each bar that rises from the dark shaded area corresponds to the turnover component.

805

Appendix S4 Sensitivity Analyses Full Results

Table S2. Sampling coverage estimates for the nine plots across the five years. SC is the sampling coverage for the observed data, and the LCI and UCI are the 95% lower and upper confidence intervals, respectively.

SC	LCI	UCI	Plot	Year	SC	LCI	UCI	Plot	Year
0.992	0.987	0.996	1	2012	0.983	0.967	1.000	8	2012
0.986	0.981	0.991	1	2013	0.987	0.981	0.993	8	2013
0.992	0.987	0.997	1	2014	0.989	0.983	0.995	8	2014
0.987	0.982	0.993	1	2015	0.981	0.968	0.993	8	2015
0.986	0.981	0.992	1	2016	0.981	0.970	0.991	8	2016
0.942	0.911	0.974	2	2012	0.979	0.965	0.992	9	2012
0.984	0.977	0.992	2	2013	0.990	0.986	0.995	9	2013
0.985	0.975	0.995	2	2014	0.985	0.976	0.993	9	2014
0.967	0.952	0.981	2	2015	0.976	0.964	0.989	9	2015
0.989	0.983	0.995	2	2016	0.973	0.958	0.987	9	2016
0.970	0.956	0.985	3	2012					
0.990	0.982	0.997	3	2013					
0.996	0.993	1.000	3	2014					
0.972	0.959	0.985	3	2015					
0.985	0.974	0.996	3	2016					
0.918	0.878	0.957	4	2012					
0.991	0.987	0.995	4	2013					
0.991	0.988	0.994	4	2014					
0.979	0.972	0.986	4	2015					
0.985	0.978	0.992	4	2016					
0.810	0.666	0.954	5	2012					
0.994	0.989	0.998	5	2013					
0.989	0.982	0.996	5	2014					
0.984	0.976	0.992	5	2015					
0.988	0.978	0.999	5	2016					
0.902	0.845	0.958	6	2012					
0.954	0.931	0.977	6	2013					
0.968	0.956	0.980	6	2014					
0.965	0.947	0.984	6	2015					
0.966	0.949	0.984	6	2016					
0.983	0.957	1.009	7	2012					
0.977	0.965	0.990	7	2013					
0.985	0.977	0.993	7	2014					
0.963	0.943	0.984	7	2015					
0.910	0.867	0.953	7	2016					

Using three SLAM traps in a single plot

Using three SLAM traps in a plot rather than one did not result in substantially different sampled communities. Species richness across the three traps in T18 only ranged 49 – 51 species, whilst abundance varied from 1380 to 1739 individuals per trap. The alpha parameter of the gambin distribution was relatively constant between the three traps (2.47, 2.44 and 3.69), indicating similar SAD shapes. 58% of the total sampled species (n = 38) were present in all three traps and overall spatial beta-diversity was low based on both presence/absence data (Sorensen dissimilarity = 0.24) and abundance data (Bray-Curtis multiple-site dissimilarity = 0.31). Thus, we are confident that our general sampling protocol is sufficient to obtain representative samples of the arthropod fauna in each plot.